

Frequency-Domain Order Parameters for the Burst And Spike Synchronization Transitions of Bursting Neurons

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Abstract

Through separation of the fast spiking and the slow bursting timescales, we charac-

terize the burst and spike synchronization transitions by varying the noise intensity D in a population of bursting neurons. Instantaneous population firing rate, $R(t)$ is used as a collective quantity describing population activities. Through frequency filtering, we decompose $R(t)$ into $R_b(t)$ (the instantaneous population burst rate (IPBR) showing the bursting behavior) and $R_s(t)$ (the instantaneous population spike rate (IPSR) showing the intraburst spiking behavior). Oscillations of R_b and R_s in the time domain are characterized by “bursting” and “spiking” peaks in their power spectral densities, respectively. Each spectral “resonance” (i.e., peak) may be analyzed in terms of a “coherence factor” β which is defined by a “signal to noise” ratio of the spectral peak height and its relative width. Then, the bursting and spiking coherence factors β_b and β_s of the bursting and spiking peaks in the power spectral densities of R_b and R_s are shown to play the role of “frequency-domain” bursting and spiking order parameters, used for characterizing the burst and spike synchronization transitions, respectively. Through calculation of β_b and β_s , we obtain the bursting and spiking noise thresholds, D_b^* and D_s^* , beyond which the burst and spike synchronizations break up, respectively. For more direct visualization of bursting behaviors, we consider another raster plot of bursting onset or offset times, from which we can directly obtain the IPBR, $R_b^{(on)}(t)$ or $R_b^{(off)}(t)$, without frequency filtering. The bursting coherence factors, $\beta_b^{(on)}$ and $\beta_b^{(off)}$, of the bursting peaks in the power spectral densities of $R_b^{(on)}(t)$ and $R_b^{(off)}(t)$ are also shown to play the role of the frequency-domain bursting order parameters for the bursting transition. All these frequency-domain bursting and spiking order parameters are usefully used for characterization of the bursting and the spiking transitions, and they supplement the conventional time-domain bursting and spiking order parameters, based

on the time-averaged fluctuations of R_b , R_s , $R_b^{(on)}(t)$ and $R_b^{(off)}(t)$.

1 Introduction

Recently, much attention has been paid to brain rhythms, observed in electrical recordings of firing activity (Buzsáki , 2006). These brain rhythms emerge via synchronization between firings of individual neurons. This kind of neural synchronization may be used for efficient sensory and cognitive processing (Wang , 2010, 2003), and it is also correlated with pathological rhythms associated with neural diseases (Uhlhaas & Singer , 2006; Traub & Whittington , 2010; Kaper et al. , 2013). Here, we are interested in characterization of population synchronization of bursting neurons in terms of neural synchrony measures (Golomb , 2007). Bursting occurs when neuronal activity alternates, on a slow timescale, between a silent phase and an active (bursting) phase of fast repetitive spikings (Rinzel , 1987; Coombes & Bressloff , 2005; Izhikevich , 2006, 2007). Due to the slow and fast timescales of bursting activity, bursting neurons exhibit two types of burst and spike synchronizations. Burst synchronization on the slow bursting timescale refers to a coherence between the active phase onset or offset times of bursting neurons, while spike synchronization on the fast spike timescale characterizes a coherence between intraburst spikes fired by bursting neurons (Rubin , 2007; Omelchenko et al. , 2010). Many recent studies on the burst and spike synchronizations have been made in several aspects (e.g., chaotic phase synchronization, transitions between different states of burst synchronization, effect of network topology, effect on information transmission, suppression of bursting synchronization, and ef-

fect of noise and coupling on the burst and spike synchronization) (Sun et al. , 2011; van Vreeswijk & Hansel , 2001; Dhamala et al. , 2004; Ivanchenko et al. , 2004; Pereira et al. , 2007; Yu et al. , 2011; Tanaka et al. , 2006; Shi & Lu , 2009, 2005; Batista et al. , 2007, 2012; Lameu et al. , 2012; Kim et al. , 2012; Kim & Lim , 2013).

In this paper, we investigate the burst and spike synchronization transitions of bursting neurons by varying the noise intensity D . Population synchronization may be well visualized in the raster plot of neural spikes which can be obtained in experiments. Instantaneous population firing rate (IPFR), $R(t)$, which is directly obtained from the raster plot of spikes, is a realistic population quantity describing collective behaviors in both the computational and the experimental neuroscience (Wang , 2010; Brunel & Hakim , 2008, 1999; Brunel , 2000; Brunel & Wang , 2003; Geisler et al. , 2005; Brunel & Hansel , 2006). This experimentally-obtainable $R(t)$ is in contrast to the ensemble-averaged potential X_G which is often used as a population quantity in the computational neuroscience, because to directly get X_G in real experiments is very difficult. To overcome this difficulty, instead of X_G , we used $R(t)$ as a population quantity, and developed a realistic order parameter, based on $R(t)$, to make practical characterization of synchronization of spiking neurons in both the computational and the experimental neuroscience (Kim & Lim , 2014). The mean square deviation of $R(t)$ plays the role of the realistic order parameter \mathcal{O} used for characterizing synchronization transition of spiking neurons. Through calculation of \mathcal{O} , one can determine the region of noise intensity D where spike synchronization occurs. In this way, synchronization transition of spiking neurons may be well characterized in terms of the realistic order parameter \mathcal{O} , based on the IPFR $R(t)$.

The main purpose of our study is to characterize the synchronization transitions of bursting neurons in terms of “frequency-domain” order parameters by extending the realistic time-domain order parameter of spiking neurons (Kim & Lim , 2014) to the case of bursting neurons. This extension work on the frequency-domain order parameters is in contrast to another extension work where the synchronization transitions of bursting neurons are characterized in terms of the conventional “time-domain” order parameters (Kim & Lim , 2014). The IPFR $R(t)$ shows the whole combined population behaviors including the burst and spike synchronizations with both the slow and fast timescales. To clearly investigate the synchronization transitions of bursting neurons, we separate the slow and fast timescales of the bursting activity via frequency filtering, and decompose the IPFR $R(t)$ into $R_b(t)$ (the instantaneous population burst rate (IPBR) describing the bursting behavior) and $R_s(t)$ and the instantaneous population spike rate (IPSR) describing the intraburst spiking behavior). For the cases of the burst and spike synchronizations, R_b and R_s exhibit oscillations, independently of N (the number of the bursting neurons). On the other hand, in the cases of the burst and spike synchronizations, R_b and R_s become stationary as N goes to the infinity. These synchronous oscillations of R_b and R_s in the time domain may be well characterized by bursting and spiking peaks of their power spectral densities. Here, we study the burst and spike synchronization transitions of the bursting neurons in the frequency domain. As in the case of the coherence resonance (Neiman , 2007), each spectral “resonance” (i.e., peak) in the power spectral density may be analyzed in terms of a “coherence factor” β (i.e., a measure of spectral coherence) which is defined by a “signal to noise” ratio of the spectral peak height and its relative width (Gang et al. , 1993; Longtin , 1997).

Then, the bursting and spiking coherence factors β_b and β_s of the bursting and spiking peaks in the power spectral densities of $R_b(t)$ and $R_s(t)$ are shown to play the role of the bursting and spiking order parameters in the frequency domain for the bursting and spiking transitions, respectively. Through calculations of these frequency-domain order parameters β_b and β_s , we determine the bursting and spiking noise thresholds, D_b^* and D_s^* , beyond which the burst and spike synchronizations of the bursting neurons disappear, respectively. We also consider another raster plot of bursting onset or offset times which visualizes the bursting behaviors more well. From this type of raster plot, we may directly obtain the IPBR, $R_b^{(on)}(t)$ or $R_b^{(off)}(t)$, without frequency filtering. Then, the bursting onset and offset coherence factors, $\beta_b^{(on)}$ and $\beta_b^{(off)}$, of the bursting onset and offset peaks in the power spectral densities of $R_b^{(on)}(t)$ and $R_b^{(off)}(t)$ are also shown to play the role of the frequency-domain bursting order parameters for the bursting transition. All these frequency-domain bursting and spiking order parameters may be usefully used for characterization of the burst and spike synchronization transitions of the bursting neurons, and they supplement the conventional time-domain bursting and spiking order parameters, based on the time-averaged fluctuations of R_b , R_s , $R_b^{(on)}(t)$ and $R_b^{(off)}(t)$ (Kim & Lim, 2014).

This paper is organized as follows. In Sec. 2, we describe an inhibitory network of bursting Hindmarsh-Rose (HR) neurons. In Sec. 3, we separate the slow bursting and the fast spiking timescales via frequency filtering, and develop realistic frequency-domain bursting and spiking order parameters (i.e., the bursting and spiking coherence factors) β_b and β_s , based on the power spectral densities of the IPBR $R_b(t)$ and the IPSR $R_s(t)$. Furthermore, without frequency filtering, we directly obtain the IPBRs

$R_b^{(on)}(t)$ and $R_b^{(off)}(t)$ from the raster plots of the bursting onset and offset times. Then, the bursting onset and offset coherence factors $\beta_b^{(on)}$ and $\beta_b^{(off)}$ of the bursting onset and offset peaks in the power spectral densities of $R_b^{(on)}(t)$ and $R_b^{(off)}(t)$ also play the role of realistic frequency-domain bursting order parameters. It is shown in explicit examples that these realistic frequency-domain bursting and spiking order parameters may be used effectively for characterization of the bursting and spiking transitions of the bursting neurons in both the computational and the experimental neuroscience. Finally, a summary is given in Section 4.

2 A Network of Inhibitory Bursting Hindmarsh-Rose Neurons

We consider an inhibitory network of N globally-coupled bursting HR neurons. The representative bursting HR neuron model was originally introduced to describe the time evolution of the membrane potential for the pond snails (Hindmarsh & Rose , 1982, 1984; Rose & Hindmarsh , 1985). The population dynamics in this inhibitory network is governed by the following set of ordinary differential equations:

$$\frac{dx_i}{dt} = y_i - ax_i^3 + bx_i^2 - z_i + I_{DC} + D\xi_i - I_{syn,i}, \quad (1)$$

$$\frac{dy_i}{dt} = c - dx_i^2 - y_i, \quad (2)$$

$$\frac{dz_i}{dt} = r [s(x_i - x_o) - z_i], \quad (3)$$

$$\frac{dg_i}{dt} = \alpha g_\infty(x_i)(1 - g_i) - \beta g_i, \quad i = 1, \dots, N, \quad (4)$$

where

$$I_{syn,i} = \frac{J}{N-1} \sum_{j(\neq i)}^N g_j(t)(x_i - X_{syn}), \quad (5)$$

$$g_\infty(x_i) = 1/[1 + e^{-(x_i - x_s^*)\delta}]. \quad (6)$$

Here, the state of the i th HR neuron at a time t (measured in units of milliseconds) is described by four state variables: the fast membrane potential x_i , the fast recovery current y_i , the slow adaptation current z_i , and the synaptic gate variable g_i representing the fraction of open synaptic ion channels. The parameters in the single HR neuron are taken as $a = 1.0$, $b = 3.0$, $c = 1.0$, $d = 5.0$, $r = 0.001$, $s = 4.0$, and $x_o = -1.6$ (Longtin, 1997).

Each bursting HR neuron is stimulated by using the common DC current I_{DC} and an independent Gaussian white noise ξ_i [see the 5th and the 6th terms in Eq. (1)] satisfying $\langle \xi_i(t) \rangle = 0$ and $\langle \xi_i(t) \xi_j(t') \rangle = \delta_{ij} \delta(t - t')$, where $\langle \dots \rangle$ denotes the ensemble average. The noise ξ is a parametric one that randomly perturbs the strength of the applied current I_{DC} , and its intensity is controlled by using the parameter D . As I_{DC} passes a threshold I_{DC}^* ($\simeq 1.26$) in the absence of noise, each single HR neuron exhibits a transition from a resting state to a bursting state. As an example, we consider the case of $I_{DC} = 1.3$. Figures 1(a)-1(b) show the time series of the fast membrane potential $x(t)$ and the fast recovery current $y(t)$, while the time series of the slow adaptation current $z(t)$ is shown in Fig. 1(c). As seen well in the time series of x and y , the bursting activity alternates, on a slow timescale, between a silent phase and an active (bursting) phase of fast repetitive spikings. Here, we consider the suprathreshold case of $I_{DC} = 1.3$ where each HR neuron exhibits spontaneous bursting activity without noise.

The last term in Eq. (1) represents the synaptic coupling of the network. $I_{syn,i}$ of

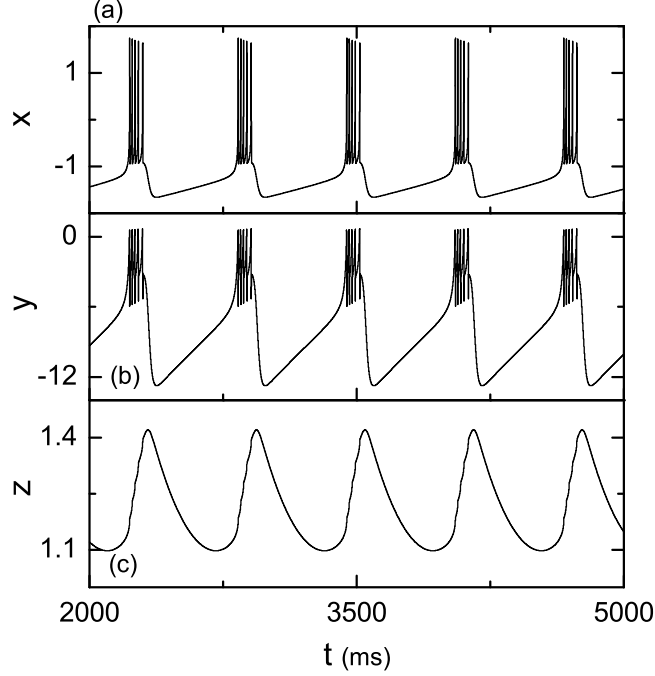


Figure 1: Single HR neuron for $I_{DC} = 1.3$ and $D = 0$. Plots of time series of (a) the fast membrane potential, (b) the fast recovery current $y(t)$, and (c) the slow adaptation current.

Eq. (5) represents a synaptic current injected into the i th neuron. Here the coupling strength is controlled by the parameter J and X_{syn} is the synaptic reversal potential. Here, we use $X_{syn} = -2$ for the inhibitory synapse. The synaptic gate variable g obeys the 1st order kinetics of Eq. (4) (Golomb & Rinzel , 1994; Wang & Buzsáki , 1996). Here, the normalized concentration of synaptic transmitters, activating the synapse, is assumed to be an instantaneous sigmoidal function of the membrane potential with a threshold x_s^* in Eq. (6), where we set $x_s^* = 0$ and $\delta = 30$ (Liang et al. , 2009). The transmitter release occurs only when the neuron emits a spike (i.e., its potential x is larger than x_s^*). For the inhibitory GABAergic synapse (involving the GABA_A receptors), the synaptic channel opening rate, corresponding to the inverse of the synaptic rise time τ_r , is $\alpha = 10 \text{ ms}^{-1}$, and the synaptic closing rate β , which is the inverse of

the synaptic decay time τ_d , is $\beta = 0.1 \text{ ms}^{-1}$ (Börger and Kopell, 2003, 2005). Hence, I_{syn} rises fast and decays slowly.

Numerical integration of Eqs. (1)-(4) is done using the Heun method (San Miguel & Toral, 2000) (with the time step $\Delta t = 0.01 \text{ ms}$). For each realization of the stochastic process, we choose a random initial point $[x_i(0), y_i(0), z_i(0), g_i(0)]$ for the i th ($i = 1, \dots, N$) neuron with uniform probability in the range of $x_i(0) \in (-2, 2)$, $y_i(0) \in (-16, 0)$, $z_i(0) \in (1.1, 1.4)$, and $g_i(0) \in (0, 1)$.

3 Frequency-Domain Order Parameters for the Burst and Spike Synchronization Transitions

In this section, we study the synchronization transitions of bursting neurons. Through frequency filtering, we separate the slow bursting and the fast spiking timescales, and develop realistic bursting and spiking order parameters, based on the power spectral densities of the IPBR $R_b(t)$ and the IPSR $R_s(t)$, in the frequency domain. Furthermore, we also introduce another frequency-domain bursting order parameters, based on the power spectral densities of the IPBRs, $R_b^{(on)}$ and $R_b^{(off)}$, which are directly obtained from the raster plots of the bursting onset and offset times. Usefulness of these realistic frequency-domain order parameters for characterization of the burst and spike synchronization transitions is shown in explicit examples.

We consider an inhibitory network of N globally-coupled bursting HR neurons for $I_{DC} = 1.3$ and fix the coupling strength at $J = 0.3$. By varying the noise intensity D , we investigate the synchronization transitions of bursting HR neurons. In computational

neuroscience, a population-averaged global potential,

$$X_G(t) = \frac{1}{N} \sum_{i=1}^N x_i(t), \quad (7)$$

is often used for describing emergence of population synchronization. In this study, we consider the population behaviors after the transient time of 2×10^3 ms. Although the global potential X_G is an important ensemble-averaged quantity to describe synchronization in computational neuroscience, it is practically difficult to directly get X_G in real experiments. To overcome this difficulty, instead of X_G , we use the IPFR which is an experimentally-obtainable population quantity used in both the experimental and the computational neuroscience (Wang , 2010; Brunel & Hakim , 2008, 1999; Brunel , 2000; Brunel & Wang , 2003; Geisler et al. , 2005; Brunel & Hansel , 2006). The IPFR is obtained from the raster plot of spikes which is a collection of spike trains of individual neurons. Such raster plots of spikes, where population synchronization may be well visualized, are fundamental data in the experimental neuroscience. The raster plots of spikes in Figs. 2(a1)-2(a5) show population states for various values of noise intensity D . To get a smooth IPFR from the raster plot of spikes, we employ the kernel density estimation (kernel smoother) (Shimazaki & Shinomoto , 2010). Each spike in the raster plot is convoluted (or blurred) with a kernel function $K_h(t)$ to get a smooth estimate of IPFR, $R(t)$:

$$R(t) = \frac{1}{N} \sum_{i=1}^N \sum_{s=1}^{n_i} K_h(t - t_s^{(i)}), \quad (8)$$

where $t_s^{(i)}$ is the s th spiking time of the i th neuron, n_i is the total number of spikes for the i th neuron, and we use a Gaussian kernel function of band width h :

$$K_h(t) = \frac{1}{\sqrt{2\pi}h} e^{-t^2/2h^2}, \quad -\infty < t < \infty. \quad (9)$$

Figures 2(b1)-2(b5) show smooth IPFR kernel estimates $R(t)$ of band width $h = 1$ ms for $D = 0, 0.01, 0.04, 0.06$ and 0.08 , respectively. For $D = 0$, clear intraburst “bands,” each of which is composed of “stripes” of spikes, appear successively at nearly regular time intervals [see Fig. 2(a1)]; a magnified 1st intraburst band is given in Fig. 3(a1). For the case of $D = 0$, both the burst synchronization [synchrony on the slow bursting timescale τ_b ($\simeq 215$ ms)] and the spike synchronization [synchrony on the fast spike timescale τ_s ($\simeq 14.6$ ms)] occur in each intraburst band. As a result of this complete synchronization, the IPFR kernel estimate $R(t)$ shows a bursting activity [i.e., fast spikings appear on a slow wave in $R(t)$], as shown in Fig. 2(b1). However, as D is increased, loss of spike synchronization occurs in each intraburst band because of smearing of spiking stripes. As an example, see the case of $D = 0.01$ where the raster plot of spikes and the IPFR kernel estimate $R(t)$ are shown in Figs. 2(a2) and 2(b2), respectively. The magnified 1st intraburst band in Fig. 3(a3) shows smearing of the spiking stripes well. Consequently, the amplitude of $R(t)$ decreases, as shown in Fig. 2(b2). As D is further increased and passes a spiking noise threshold D_s^* ($\simeq 0.032$), complete loss of spike synchronization occurs in each intraburst band. Hence, only the burst synchronization (without spike synchronization) occurs, as shown in the case of $D = 0.04$ in Figs. 2(a3) and 2(b3). For this case, $R(t)$ shows a slow-wave oscillation without spikes. With increase in D , such “incoherent” intraburst bands become more and more smeared, and hence the degree of burst synchronization decreases [e.g., see the case of $D = 0.06$ in Figs. 2(a4) and 2(b4)]. As a result, the amplitude of $R(t)$ is further decreased. With further increasing D , incoherent intraburst bands begin to overlap, which eventually results in the complete loss of burst synchronization as D passes

a bursting noise threshold D_b^* ($\simeq 0.068$). In this way, completely unsynchronized states with nearly stationary $R(t)$ appear, as shown in the case of $D = 0.08$ in Figs. 2(a5) and 2(b5).

The (above) IPFR kernel estimate $R(t)$ is a population quantity describing the “whole” combined collective behaviors (including both the burst and spike synchronizations) of bursting neurons with both the slow bursting and the fast spiking timescales. Through frequency filtering, we separate the slow and the fast timescales, and decompose the IPFR kernel estimate $R(t)$ into the IPBR $R_b(t)$ and the IPSR $R_s(t)$ for more clear investigation of the burst and spike synchronizations. Through band-pass filtering of $R(t)$ [with the lower and the higher cut-off frequencies of 3 Hz (high-pass filter) and

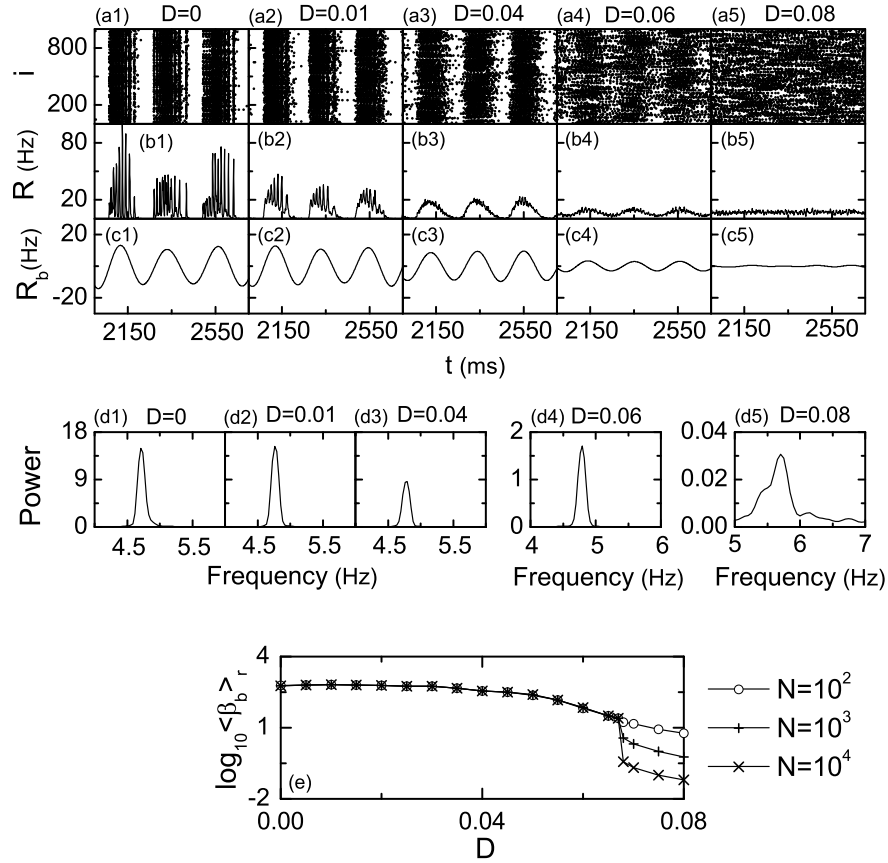


Figure 2: Population bursting states for various values of D in an inhibitory ensemble of N globally-coupled bursting HR neurons for $I_{DC} = 1.3$ and $J = 0.3$: synchronized bursting states for $D = 0, 0.01, 0.04$, and 0.06 , and unsynchronized bursting state for $D = 0.08$. $N = 10^3$ except for the case of (e). Raster plots of neural spikes for (a1)-(a5), time series of IPFR kernel estimate $R(t)$ (the band width h of the Gaussian kernel function is 1 ms) for (b1)-(b5), time series of band-pass filtered IPBR $R_b(t)$ [lower and higher cut-off frequencies of 3 Hz (high-pass filter) and 7 Hz (low-pass filter)] for (c1)-(c5), and one-sided power spectra of $\Delta R_b(t) [= R_b(t) - \overline{R_b(t)}]$ with mean-squared amplitude normalization for (d1)-(d5). Each power spectrum in (d1)-(d5) is made of 2^{15} data points and it is smoothed by the Daniell filters of lengths 3 and 5. (e) Plots of realistic frequency-domain bursting order parameter $\langle \beta_b \rangle_r$ versus D : $\langle \beta_b \rangle_r$ is obtained through average over 20 realizations for each D .

7 Hz (low-pass filter)], we get the regularly-oscillating IPBR $R_b(t)$ (containing only the slow wave without spikes) in Figs. 2(c1)-2(c5) for $D = 0, 0.01, 0.04, 0.06$, and 0.08 . As D is increased, the amplitude of $R_b(t)$ decreases gradually, and eventually $R_b(t)$ becomes nearly stationary when D passes the bursting noise threshold D_b^* ($\simeq 0.068$). We note that synchronous oscillations of $R_b(t)$ in the time domain are characterized by the bursting peaks in the power spectral densities of $\Delta R_b(t) [= R_b(t) - \overline{R_b(t)}]$, where the overline represents the time average. Figures 2(d1)-2(d5) show distinct bursting peaks in the power spectra of $\Delta R_b(t)$; each power spectrum is made of 2^{15} data points and smoothed through the Daniell filters of length 3 and 5 (Bloomfield, 2000). Then, each bursting peak may be analyzed well in terms of a bursting coherence factor β_b defined by the product of the height H_p and the Q factor of the peak (Neiman, 2007; Gang et al., 1993; Longtin, 1997):

$$\beta_b = H_p Q; Q = f_p / \Delta f_p. \quad (10)$$

Here, H_p and f_p are the height and the frequency of the bursting peak, and Δf_p is the width of the bursting peak at the height of $e^{-1/2} h$. For more accurate results, we repeat

the process to get the bursting coherence factor β_b for multiple realizations. Thus, we obtain $\langle \beta_b \rangle_r$ (average bursting coherence factor) through average over 20 realizations. Figure 2(e) shows plots of the average bursting coherence factor $\langle \beta_b \rangle_r$ versus D . For $D < D_b^*$ ($\simeq 0.068$), synchronized bursting states exist because the values of $\langle \beta_b \rangle_r$ become saturated to non-zero limit values in the thermodynamic limit of $N \rightarrow \infty$ (i.e., bursting peaks persist, independently of N). However, as D passes the bursting noise threshold D_b^* , the average bursting coherence factor $\langle \beta_b \rangle_r$ tends to zero as $N \rightarrow \infty$ (i.e., eventually bursting peaks disappear in the thermodynamic limit), and hence a transition to unsynchronized bursting states occurs because the noise spoils the burst synchronization completely. In this way, the average bursting coherence factor $\langle \beta_b \rangle_r$ describes the burst synchronization transition well in the frequency domain, and hence it plays the role of the realistic bursting order parameter in the frequency domain for the bursting transition (i.e., one can determine the bursting noise threshold D_b^* through calculation of $\langle \beta_b \rangle_r$). This frequency-domain bursting order parameter $\langle \beta_b \rangle_r$ is in contrast to the time-domain bursting order parameter, based on the time-averaged fluctuation of the IPBR $R_b(t)$ (Kim & Lim, 2014).

From now on, we investigate the intraburst spike synchronization transition of bursting HR neurons by varying the noise intensity D . Figures 3(a1)-3(a5) and Figures 3(b1)-3(b5) show the raster plots of intraburst spikes and the corresponding (band-pass filtered) IPSR $R(t)$ during the 1st global bursting cycle of the IPBR $R_b(t)$, respectively for various values of D : synchronized spiking states for $D = 0, 0.005, 0.01$, and 0.02 , and unsynchronized spiking state for $D = 0.06$. Here, the IPSRs $R_s(t)$ are obtained through band-pass filtering of the IPFR kernel estimate $R(t)$ [with the lower and

the higher cut-off frequencies of 30 Hz (high-pass filter) and 90 Hz (low-pass filter)]. Then, the intraburst spike synchronization may be well described in terms of $R_s(t)$. For $D = 0$, clear 8 spiking stripes (composed of spikes and indicating population spike synchronization) appear in the intraburst band of the 1st global bursting cycle of $R_b(t)$ in Fig. 3(a1), and the band-pass filtered IPSR $R_s(t)$ shows only the fast spiking oscillations (without a slow wave) with the population spiking frequency f_s ($\simeq 68.5$ Hz) in Fig. 3(b1). However, as D is increased, spiking stripes in the intraburst band become more and more smeared (e.g., see the cases of $D = 0.005$, 0.01 , and 0.02). Consequently, the amplitude of $R_s(t)$ decreases due to loss of spike synchronization. Eventually, when D passes the spiking noise threshold D_s^* ($\simeq 0.032$), spikes become

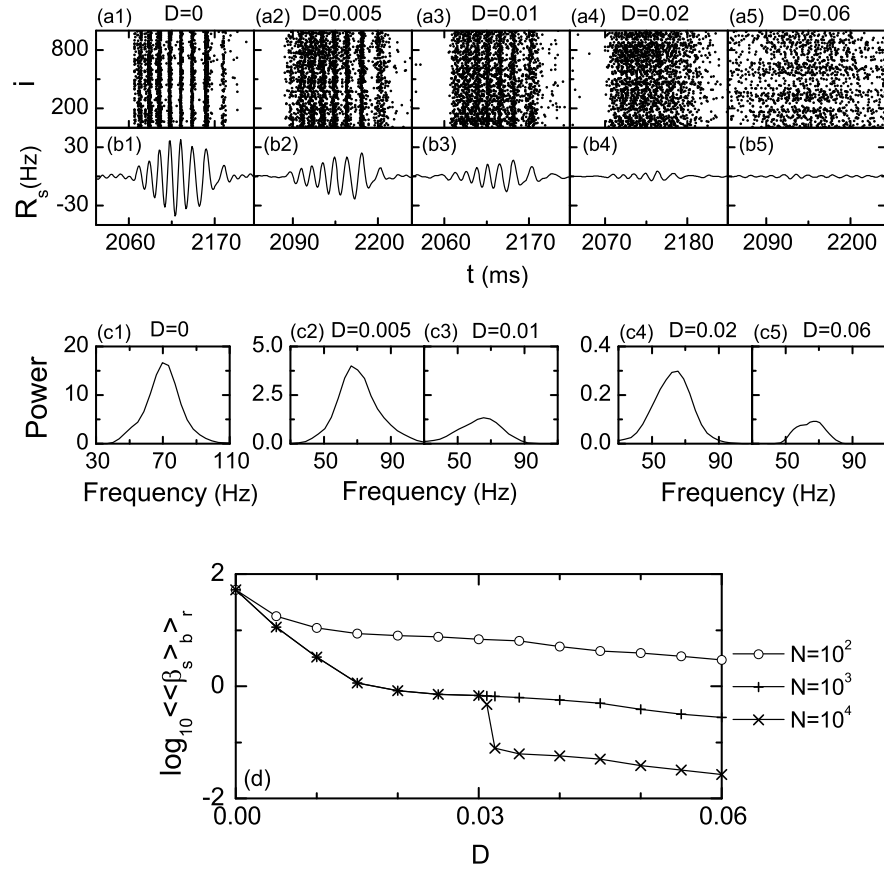


Figure 3: Population intraburst spiking states for various values of D in an inhibitory ensemble of N globally-coupled bursting HR neurons for $I_{DC} = 1.3$ and $J = 0.3$: synchronized spiking states for $D = 0, 0.005, 0.01$, and 0.02 , and unsynchronized spiking state for $D = 0.06$. $N = 10^3$ except for the case of (d). Raster plots of neural spikes for (a1)-(a5) and time series of the band-pass filtered IPSR $R_s(t)$ [lower and higher cut-off frequencies of 30 Hz (high-pass filter) and 90 Hz (low-pass filter)] for (b1)-(b5) in the 1st global bursting cycle of the IPBR $R_b(t)$ (after the transient time of 2×10^3 ms) for each D . (c1)-(c5) one-sided power spectra of $\Delta R_s(t) [= R_s(t) - \overline{R_s(t)}]$ with mean-squared amplitude normalization. Each power spectrum in (c1)-(c5) is made of 2^8 data points for each global bursting cycle of $R_b(t)$ and it is smoothed by the Daniell filters of lengths 3 and 5. (d) Plots of realistic frequency-domain spiking order parameter $\langle\langle\beta_s\rangle_b\rangle_r$ versus D ; $\langle\langle\beta_s\rangle_b\rangle_r$ is obtained through double-averaging over the 20 bursting cycles and the 20 realizations.

completely scattered within the intraburst band, and $R_s(t)$ becomes nearly stationary. Consequently, for $D > D_s^*$, complete loss of spike synchronization occurs in the intraburst band, as shown in Fig. 3(b5) for $D = 0.06$. Figures 3(c1)-3(c5) show the power spectra of $\Delta R_s(t) [= R_s(t) - \overline{R_s(t)}]$ in the 1st global bursting cycle of $R_b(t)$: each power spectrum is made of 2^8 data points and smoothed through the Daniell filters of length 3 and 5. Spiking peaks in their power spectra are analyzed in terms of the spiking coherence factors β_s (defined by the product of the height h and the Q factor of the peak). For more accurate results, we repeat the process to get β_s for multiple realizations. In each realization we follow the 20 global bursting cycles of $R_b(t)$, and get the double-averaged spiking coherence factor $\langle\langle\beta_s\rangle_b\rangle_r$ through average over 20 realizations. Figure 3(d) shows plots of the double-averaged spiking coherence factor $\langle\langle\beta_s\rangle_b\rangle_r$ versus D . For $D < D_s^*$ ($\simeq 0.032$), synchronized spiking states exist because the values of $\langle\langle\beta_s\rangle_b\rangle_r$ become saturated to non-zero limit values as $N \rightarrow \infty$ (i.e., spiking peaks persist, irrespectively of N). However, when D passes the spiking noise threshold D_s^* ,

$\langle\langle\beta_s\rangle_b\rangle_r$ tends to zero in the thermodynamic limit of $N \rightarrow \infty$ (i.e., eventually spiking peaks disappear in the thermodynamic limit), and hence a transition to unsynchronized spiking states occurs because the noise spoils the intraburst spike synchronization completely. In this way, the double-averaged spiking coherence factor $\langle\langle\beta_s\rangle_b\rangle_r$ describes the intraburst spike synchronization transition well in the frequency domain, and hence it plays the role of the realistic spiking order parameter in the frequency domain for the spiking transition (i.e., one can determine the spiking noise threshold D_s^* through calculation of $\langle\beta_b\rangle_r$). This frequency-domain spiking order parameter is also in contrast to the time-domain spiking order parameter, based on the time-averaged fluctuation of the IPSR $R_s(t)$ (Kim & Lim, 2014).

Finally, we consider another raster plot of bursting onset or offset times for more direct visualization of bursting behavior. [At the onset (offset) times of the i th bursting HR neuron, its individual potential x_i passes the threshold of $x_b^* = -1$ from below (above).] Without frequency filtering, we can directly obtain the IPBR kernel estimate, $R_b^{(on)}(t)$ [$R_b^{(off)}(t)$] from the raster plot of the bursting onset (offset) times. Figures 4(a1)-4(a5) show the raster plots of the bursting onset times for various values of D , while the raster plots of the bursting offset times are shown in Figs. 4(c1)-4(c5). From these raster plots of the bursting onset (offset) times, we obtain smooth IPBR kernel estimates, $R_b^{(on)}(t)$ [$R_b^{(off)}(t)$], of band width $h = 50$ ms in Figs. 4(b1)[(d1)]-4(b5)[(d5)] for $D = 0, 0.01, 0.04, 0.06$, and 0.08 . For $D = 0$, clear bursting “stripes” [composed of bursting onset (offset) times and indicating burst synchronization] appear successively at nearly regular time intervals; the bursting onset and offset stripes are time-shifted [see Figs. 4(a1) and 4(c1)]. The corresponding IPBR kernel estimates, $R_b^{(on)}(t)$ and $R_b^{(off)}(t)$, for $D = 0$

show regular oscillations with the same population bursting frequency $f_b (\simeq 4.7 \text{ Hz})$, although they are phase-shifted [see Figs. 4(b1) and 4(d1)]. With increasing D , the bursting onset and offset stripes in the raster plots become smeared and begin to overlap, and thus the degree of the burst synchronization decreases. As a result, the amplitudes of both $R_b^{(on)}(t)$ and $R_b^{(off)}(t)$ decrease gradually (e.g., see the cases of $D = 0.01$, 0.04, and 0.06). Eventually, as D passes the bursting noise threshold $D_b^* (\simeq 0.068)$, bursting onset and offset times become completely scattered in the raster plots, and the

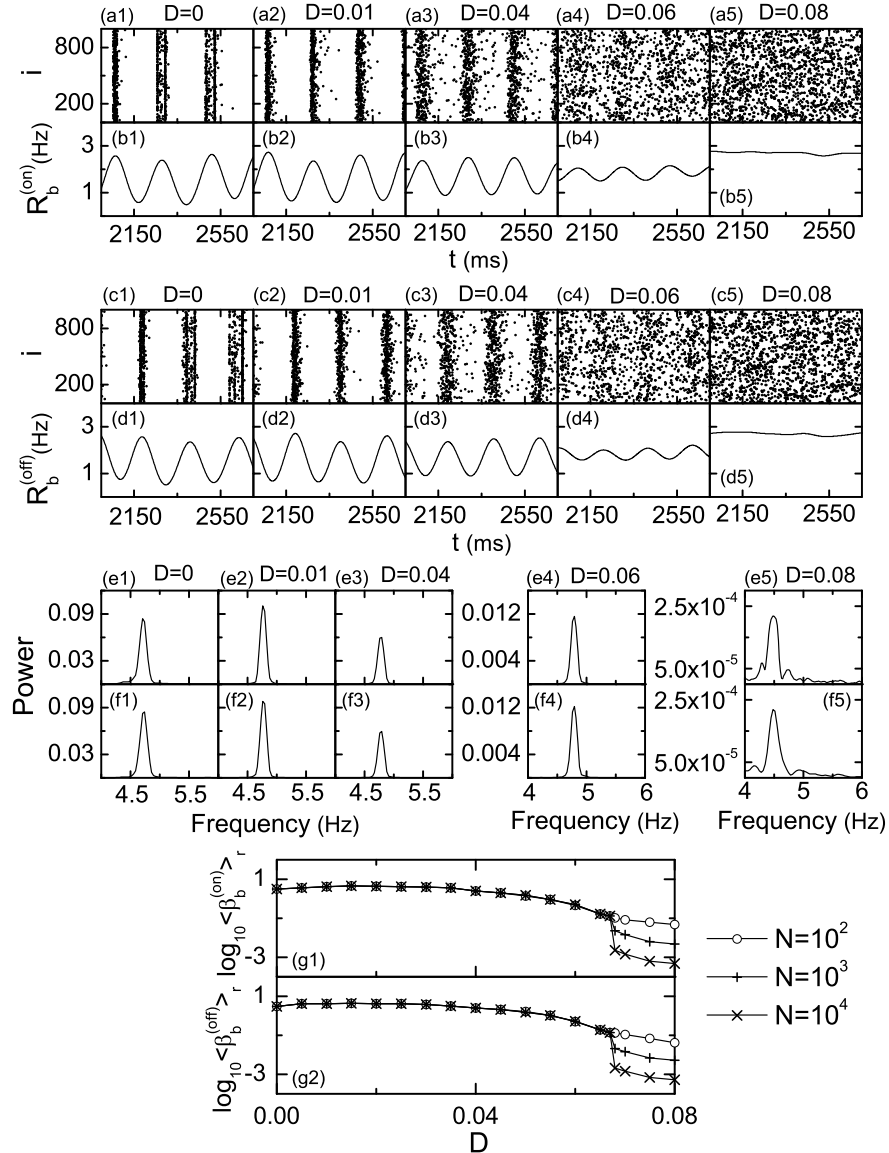


Figure 4: Population bursting states represented by the active phase onset and offset times for various values of D in an inhibitory ensemble of N globally-coupled bursting HR neurons for $I_{DC} = 1.3$ and $J = 0.3$: synchronized bursting states for $D = 0, 0.01, 0.04$, and 0.06 , and unsynchronized bursting state for $D = 0.08$. $N = 10^3$ except for the cases of (g1) and (g2). Raster plot of the bursting onset times for (a1)-(a5) and time series of the IPBR $R_b^{(on)}(t)$ (the band width h of the Gaussian kernel function is 50 ms) for (b1)-(b5). Raster plot of the bursting offset times for (c1)-(c5) and time series of the IPBR $R_b^{(off)}(t)$ (the band width h of the Gaussian kernel function is 50 ms) for (d1)-(d5). (e1)-(e5) One-sided power spectra of $\Delta R_b^{(on)}(t) [= R_b^{(on)}(t) - \overline{R_b^{(on)}}(t)]$ with mean-squared amplitude normalization and (f1)-(f5) one-sided power spectra of $\Delta R_b^{(off)}(t) [= R_b^{(off)}(t) - \overline{R_b^{(off)}}(t)]$ with mean-squared amplitude normalization. Each power spectrum is made of 2^{15} data points and it is smoothed by the Daniell filters of lengths 3 and 5. Plots of realistic frequency-domain bursting order parameters (g1) $\langle \beta_b^{(on)} \rangle_r$ and (g2) $\langle \beta_b^{(off)} \rangle_r$ versus D : $\langle \beta_b^{(on)} \rangle_r$ and $\langle \beta_b^{(off)} \rangle_r$ are obtained through average over 20 realizations for each D .

corresponding IPBR kernel estimates, $R_b^{(on)}(t)$ and $R_b^{(off)}(t)$, become nearly stationary, as shown in Figs. 4(b5) and 4(d5) for $D = 0.08$. Figures 4(e1)-4(e5) show the power spectra of $\Delta R_s^{(on)}(t) [= R_s^{(on)}(t) - \overline{R_s^{(on)}}(t)]$, while Figures 4(f1)-4(f5) show the power spectra of $\Delta R_s^{(off)}(t) [= R_s^{(off)}(t) - \overline{R_s^{(off)}}(t)]$; each power spectrum is made of 2^{15} data points and smoothed through the Daniell filters of length 3 and 5. Bursting onset and offset peaks in these power spectra are analyzed in terms of the bursting onset and offset coherence factors $\beta_b^{(on)}$ and $\beta_b^{(off)}$ (each coherence factor of a peak is defined by the product of the height h and the Q factor of the peak). For more accurate results, we repeat the process to obtain $\beta_b^{(on)}$ and $\beta_b^{(off)}$ for multiple realizations. Thus, we obtain $\langle \beta_b^{(on)} \rangle_r$ (average bursting onset coherence factor) and $\langle \beta_b^{(off)} \rangle_r$ (average bursting offset coherence factor) through average over 20 realizations. Figures 4(g1) and 4(g2) show plots of the average bursting onset and offset coherence factor $\langle \beta_b^{(on)} \rangle_r$ and $\langle \beta_b^{(off)} \rangle_r$ versus D , respectively. As in the case of the (above) average bursting coherence factor

$\langle \beta_b \rangle_r$, when passing the same bursting noise threshold D_b^* ($\simeq 0.068$), both the average bursting onset and offset coherence factors $\langle \beta_b^{(on)} \rangle_r$ and $\langle \beta_b^{(off)} \rangle_r$ go to zero as $N \rightarrow \infty$ (i.e., eventually bursting onset and offset peaks disappear in the thermodynamic limit), and hence a transition to burst unsynchronization occurs for $D > D_b^*$, because the noise breaks up the burst synchronization completely. In this way, both the average bursting onset and offset coherence factors, $\langle \beta_b^{(on)} \rangle_r$ and $\langle \beta_b^{(off)} \rangle_r$, describe the burst synchronization transition well in the frequency domain, and hence they also play the role of the realistic bursting order parameters in the frequency domain for the bursting transition together with $\langle \beta_b \rangle_r$. These frequency-domain bursting order parameters are also in contrast to the time-domain bursting order parameters, based on the time-averaged fluctuations of $R_b^{(on)}(t)$ and $R_b^{(off)}(t)$ (Kim & Lim, 2014).

4 Summary

We have investigated the burst and spike synchronization transitions of bursting HR neurons by varying the noise intensity D . Population synchronization may be well visualized in the raster plot of neural spikes which may be obtained in experiments. The IPFR kernel estimate $R(t)$, which is obtained from the raster plot of spikes, is a realistic collective quantity describing the whole combined population behaviors (including both the burst and spike synchronization) with the slow bursting and the fast spiking timescales. Through frequency filtering, we have decomposed the IPFR kernel estimate $R(t)$ into the IPBR $R_b(t)$ and the IPSR $R_s(t)$. We note that both $R_b(t)$ and $R_s(t)$ may be used to effectively characterize the burst and spike synchronizations, respectively.

For synchronous cases, oscillations of R_b and R_s in the time domain are characterized by the bursting and spiking peaks in their power spectral densities. Similar to the case of coherence resonance, each spectral resonance (i.e., peak) may be analyzed in terms of the coherence factor β . The average bursting and spiking coherence factors $\langle\beta_b\rangle_r$ and $\langle\langle\beta_s\rangle_b\rangle_r$ of the bursting and spiking peaks in the power spectral densities of ΔR_b and ΔR_s have been found to play the role of the frequency-domain bursting and spiking order parameters for the burst and spike synchronization transitions, respectively. By calculating $\langle\beta_b\rangle_r$ and $\langle\langle\beta_s\rangle_b\rangle_r$, we have determined the noise bursting and spiking thresholds, D_b^* and D_s^* , beyond which the burst and spike synchronizations break up, respectively. For more direct visualization of bursting behavior, we consider another raster plot of bursting onset or offset times, from which the IPBR, $R_b^{(on)}(t)$ or $R_b^{(off)}(t)$, can be directly obtained without frequency filtering. Then, the average bursting onset and offset coherence factors, $\langle\beta_b^{(on)}\rangle_r$ and $\langle\beta_b^{(off)}\rangle_r$ of the bursting onset and offset peaks in the power spectral densities of $\Delta R_b^{(on)}(t)$ and $\Delta R_b^{(off)}(t)$ have also been shown to play the role of the frequency-domain bursting order parameters for the bursting transition. In this way, the frequency-domain bursting and spiking order parameters may be usefully used for characterizing the burst and and spike synchronization transitions of the bursting neurons, and they supplement the conventional time-domain bursting and spiking order parameters (Kim & Lim , 2014).

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References

- Batista C.A.S., Batista A.M., de Pontes J.A.C., Viana R.L., & Lopes S.R. (2007). Chaotic phase synchronization in scale-free networks of bursting neurons. *Phys. Rev. E*, 76, 016218.
- Batista C.A.S., Lameu E.L., Batista A.M., Lopes S.R., Pereira T., Zamora-Lopez G., Kurths J., & Viana R.L. (2012). Phase synchronization of bursting neurons in clustered small-world networks. *Phys. Rev. E*, 86, 016211.
- Bloomfield P. (2000). *Fourier analysis of time series: an introduction*, 2nd edition (New York, John Wiley & Sons Inc.), p. 261.
- Börger C. & Kopell N. (2003). Synchronization in network of excitatory and inhibitory neurons with sparse, random connectivity. *Neural Comput.*, 15, 509-538.
- Börger C. & Kopell N. (2005). Effects of noisy drive on rhythms in networks of excitatory and inhibitory neurons. *Neural Comput.*, 17, 557-608.
- Brunel N. (2000). Dynamics of sparsely connected networks of excitatory and inhibitory spiking neurons. *J. Comput. Neurosci.*, 8, 183-208.
- Brunel N. & Hakim V. (1999). Fast global oscillations in networks of integrate-and-fire neurons with low firing rates. *Neural Comput.*, 11, 1621-1671.
- Brunel N. & Hakim V. (2008). Sparsely synchronized neuronal oscillations. *Chaos*, 18, 015113.

- Brunel N. & Hansel D. (2006). How noise affects the synchronization properties of recurrent networks of inhibitory neurons. *Neural Comput.*, 18, 1066-1110.
- Brunel N. & Wang X.-J. (2003). What determines the frequency of fast network oscillations with irregular neural discharges? I. Synaptic dynamics and excitation-inhibition balance. *J. Neurophysiol.*, 90, 415-430.
- Buzsáki G. (2006). *Rhythms of the Brain*. New York: Oxford University Press.
- Coombes S. & Bressloff P.C. (Eds.) (2005). *Bursting: The Genesis of Rhythm in the Nervous System*. Singapore: World Scientific.
- Dhamala M., Jirsa V., & Ding M. (2004). Transitions to synchrony in coupled bursting neurons. *Phys. Rev. Lett.*, 92, 028101.
- Gang H., Ditzinger T., Ning C.Z., & Haken H. (1993). Stochastic resonance without external periodic force. *Phys. Rev. Lett.*, 71, 807-810.
- Geisler C., Brunel N., & Wang X.-J. (2005). The contribution of intrinsic membrane dynamics to fast network oscillations with irregular neuronal discharges. *J. Neurophysiol.*, 94, 4344-4361.
- Golomb D. (2007). Neuronal synchrony measures. *Scholarpedia*, 2(1), 1347.
- Golomb D. & Rinzel J. (1994). Clustering in globally coupled inhibitory neurons. *Physica D*, 72, 259-282.
- Hindmarsh J.L. & Rose R.M. (1982). A model of the nerve impulse using two first-order differential equations. *Nature*, 296, 162-164.

- Hindmarsh J.L. & Rose R.M. (1984). A model of neuronal bursting using three coupled first order differential equations. *Proc. R. Soc. London, Ser. B*, 221, 87-102.
- Ivanenko M.V., Osipov G.V., Shalfeev V.D., & Kurths J. (2004). Phase synchronization in ensembles of bursting oscillators. *Phys. Rev. Lett.*, 93, 134101.
- Izhikevich E.M. (2006). Bursting. *Scholarpedia*, 1(3), 1300.
- Izhikevich E.M. (2007). *Dynamical Systems in Neuroscience*. Cambridge: MIT Press.
- Kaper T.J., Kramer M.A., & Rotstein H.G. (2013). Introduction to focus issue: rhythms and dynamic transitions in neurological disease: modeling, computation, and experiment. *Chaos*, 23, 046001.
- Kim S.-Y. & Lim W. (2013). Coupling-induced population synchronization in an excitatory population of subthreshold Izhikevich neurons. *Cognitive Neurodynamics*, 7, 495-503.
- Kim S.-Y. & Lim W. (2014). Realistic thermodynamic and statistical-mechanical measures for neural synchronization. *J. Neurosci. Methods*, 226, 161-170.
- Kim S.-Y. & Lim W. (2014). Thermodynamic and statistical-mechanical measures for characterization of the burst and spike synchronizations of bursting neurons (submitted for publication in *J. Neurosci. Methods*). arXiv:1403.3994.
- Kim S.-Y., Kim Y., Hong D.G., Kim J., & Lim W. (2012). Stochastic bursting synchronization in a population of subthreshold Izhikevich neurons. *J. Korean Phys. Soc.*, 60, 1441-1447.

- Lameu E.L., Batista C.A.S., Batista A.M., Larosz K., Viana R.L., Lopes S.R., & Kurths J. (2012). Suppression of bursting synchronization in clustered scale-free (rich-club) neural networks. *Chaos*, 22, 043149.
- Liang X., Tang M., Dhamala M., & Liu Z. (2009). Phase synchronization of inhibitory bursting neurons induced by distributed time delays in chemical coupling. *Phys. Rev. E*, 80, 066202.
- Longtin A. (1997). Autonomous stochastic resonance in bursting neurons. *Phys. Rev. E*, 55, 868-876.
- Neiman A. (2007). Coherence resonance. *Scholarpedia*, 2(11), 1442.
- Omelchenko I., Rosenblum M., & Pikovsky A. (2010). Synchronization of slow-fast systems. *Eur. Phys. J.*, 191, 3-14.
- Pereira T., Baptista M., & Kurths J. (2007). Multi-time-scale synchronization and information processing in bursting neuron networks. *Eur. Phys. J. Spec. Top.*, 146, 155-168.
- Rinzel J. (1987). A formal classification of bursting mechanisms in excitable systems. In Teramoto E. & Yamaguti M. (Eds.), *Mathematical Topics in Population Biology, Morphogenesis, and Neurosciences*, vol. 71 of *Lecture Notes in Biomathematics*. Berlin: Springer-Verlag.
- Rose R.M. & Hindmarsh J.L. (1985). A model of a thalamic neuron. *Proc. R. Soc. London Ser. B*, 225, 161-193.
- Rubin J.E. (2007). Burst synchronization. *Scholarpedia*, 2(10), 1666.

- San Miguel M. & Toral R. (2000). In Martinez J., Tiemann R., & Tirapegui E. (Eds.), *Instabilities and Nonequilibrium Structures VI*. Dordrecht: Kluwer Academic Publisher, p.35.
- Shi X. & Lu Q. (2005). Firing patterns and complete synchronization of coupled Hindmarsh-Rose neurons. *Chin. Phys.*, *14*, 77-85.
- Shi X. & Lu Q. (2009). Burst synchronization of electrically and chemically coupled map-based neurons. *Physica A*, *388*, 2410-2419.
- Shimazaki H. & Shinomoto S. (2010). Kernel band width optimization in spike rate estimation. *J. Comput. Neurosci.*, *29*, 171-182.
- Sun X., Lei J., Perc M., Kurths J., & Chen G. (2011). Burst synchronization transitions in a neuronal network of subnetworks. *Chaos*, *21*, 016110.
- Tanaka G., Ibarz B., Sanjuan M.A., & Aihara K. (2006). Synchronization and propagation of bursts in networks of coupled map neurons. *Chaos*, *16*, 013113.
- Traub R.D. & Whittington M.A. (2010). *Cortical Oscillations in Health and Diseases*. New York: Oxford University Press.
- Uhlhaas P.J. & Singer W. (2006). Neural synchrony in brain disorders: relevance for cognitive dysfunctions and pathophysiology. *Neuron*, *52*, 155-168.
- van Vreeswijk C. & Hansel D. (2001). Patterns of synchrony in neural networks with adaptation. *Neural Comput.*, *13*, 959-992.
- Wang X.-J. (2003). In Nadel L. (Ed.), *Encyclopedia of Cognitive Science*. London: MacMillan, pp. 272-280.

- Wang X.-J. (2010). Neurophysiological and computational principles of cortical rhythms in cognition. *Physiol. Rev.*, *90*, 1195-1268.
- Wang X.-J. & Buzsáki G. (1996). Gamma oscillations by synaptic inhibition in a hippocampal interneuronal network. *J. Neurosci.*, *16*, 6402-6413.
- Yu H., Wang J., Deng B., Wei X., Wong Y.K., Chan W.L., Tsang K.M., & Yu Z. (2011). Chaotic phase synchronization in small world networks of bursting neurons. *Chaos*, *21*, 013127.